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The flash-lag effect is reduced when the flash is perceived as a sensory consequence of our action

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Abstract

The flash-lag effect (FLE) is defined as an error in localization that consists of perceiving a flashed object to lag behind a moving one when both are presented in physical alignment. Previous studies have addressed the question if it is the predictability of the flash, or the moving object, that modulates the amount of the error. However, the case when the flash is self-generated, and hence can be internally predicted, has not yet been addressed. In Experiment 1, we compare four conditions: flash unpredictable, flash externally predicted by a beep, flash internally generated (and predicted) by pressing a key, and flash triggered by a key press but temporally unpredictable. The FLE was significantly reduced only when the flash was internally predictable. In Experiment 2, we rule out the possibility that the reduction of the FLE was due to the use of the key press as a temporal marker. We conclude that when the flash is perceived as a sensory consequence of our own action, its detection can be speeded up, thereby resulting in a reduction of the FLE. A third experiment supports this interpretation. The mechanism by virtue of which the detection is accelerated could be related to efferent signals from motor areas predicting the sensory consequences of our actions.

Keywords: Flash-lag; Time; Space; Sensory consequences; Action

1. Introduction

In daily life, our visual system has to continuously update moving object positions to successfully interact with them. This is not a trivial task for the brain to perform. The diversity of localization errors when moving and static objects come into play illustrates how complex the processes underlying this task can be (see Whitney, 2002 for a complete review). A well known mislocalization visual phenomenon is the flash-lag effect (FLE). When an object is abruptly flashed in (retinal) alignment with a second moving object, the former is perceived to lag the moving object (see Nijhawan, 2002 for a review of different accounts). Although the FLE implies a mislocalization (spatial) error, a large contribution to the FLE might originate from an error in the temporal dimension. In other words, part of the mislocalization can be due to a temporal error (Brenner & Smeets, 2000; Murakami, 2001; but see Kreegipuu & Allik, 2004, for a different interpretation). For example, according to the position sampling model (Brenner & Smeets, 2000) ascertaining the position of the moving object takes time and can only be made after the flash (as a time-marker) has been perceived. Therefore, one can match the respective positions of the flash and the moving object, but only at different times. Similarly, for the differential latencies explanation (Whitney & Murakami, 1998), the extra-time needed by the visual system to perceive the flash with respect to the moving object would also result in a temporal error. However, temporal and spatial factors may contribute to the FLE. A recent study by Vreven and Verghese (2005) shows that the spatial predictability of the flash can reduce the FLE, and that the magnitude of reduction can be even larger than that obtained with a temporal cue. On the other hand, there is evidence that points to an enhancement of the FLE when either

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the unpredictability of the flash (Baldo, Kihara, Namba, & Klein, 2002; Eagleman & Sejnowski, 2000), or the moving object is increased (Kanai, Sheth, & Shimojo, 2004). Summing up, previous results show that helping subjects predict the flash, or the position of the moving object, by external means (e.g., external cues or other stimulus manipulations) has an effect on the magnitude of the FLE.

Previous studies, however, have not addressed whether the internal prediction of the flash has an effect on the FLE. In this study, we will focus on whether helping the observers anticipate in different ways *when* the flash will appear affects the magnitude of the FLE. In a first experiment, we show that external and internal prediction of the flash increase the sensitivity, but, only the latter reduces the FLE in a significant way. The results of Experiments 2 and 3 point to a possible mechanism that could account for this reduction of the FLE. To anticipate, we invoke mechanisms that, by predicting the flash as a sensory consequence of self-actions, affect the threshold for detecting incoming sensory events.

2. Experiment 1

In this experiment, we will measure the magnitude of the FLE for two different kinds of temporal predictions: an external auditory cue that predicts the flash and when flash is self-triggered.

2.1. Methods

2.1.1. Subjects

Four subjects with normal or corrected-to-normal vision participated in the experiment. All of them were naive with respect to the aims of the experiment except for the second author.

2.1.2. Stimuli

Stimuli (see Fig. 1) were displayed on a Philips 22 in monitor (Brilliance 202P4) at a refresh rate of 118 Hz and screen resolution of 1154×864 pixels. A moving bar rotated clockwise or counter-clockwise, on a trial-to-trial basis, and was divided by a visual gap located at 4.2° from fixation. A flash was shown for one frame (8.33 ms) at some point along the imaginary circle centered at the fixation red point and passing through the middle of the visual gap of the moving line. Nine angular offsets of the flash with respect to the moving bar were used, and were independently chosen for each of six possible speeds to give a psychometric function. The bar could move at six different angular speeds: 38, 68, 99, 129, 160, and 190°/s that corresponded with the following nine tangential velocities of the tip of the rotating bar: 2.98, 5.34, 7.78, 10.13, 12.57, and 14.92°/s. The luminance of the flash and of the moving bar were subjectively equated by using Quest (Watson & Pelli, 1983).

2.1.3. Procedure

The experiment consisted of four conditions. In the *control* condition the flash was shown between 2.5 and 5.8 s after the bar started to move. The location of the flash relative to the bar and the speed of the bar were varied according to the procedure of the method of constant stimuli: the 54 stimuli (6 velocities * 9 offsets) were delivered in random order until all 54 had been presented. Then, the 54 stimuli were again randomized and all presented again, and so on. Observers had to report whether the flash was leading or trailing the moving bar by pressing one of two mouse buttons. The same response was recorded in all the conditions. In a second condition, the flash was self-triggered by the observers by pressing the spacebar. After the bar started move subjects could trigger the flash by pressing the spacebar at a time of their own choice. Subjects were told that the key press would not function if they pressed the button too early (less than 2 s after the bar started to move). This was so to allow for a duration of the motion trajectory comparable to that of the *control* condition. After the subjects pressed the spacebar, the flash appeared in one of the nine angular offsets relative to the rotating bar, therefore, the relative position of the flash with respect to the rotating bar was totally independent of the time of the key press. The different velocities and angular offsets were presented exactly as in the *control* condition. The same type of response as in the control condition was recorded with the mouse. The mouse click

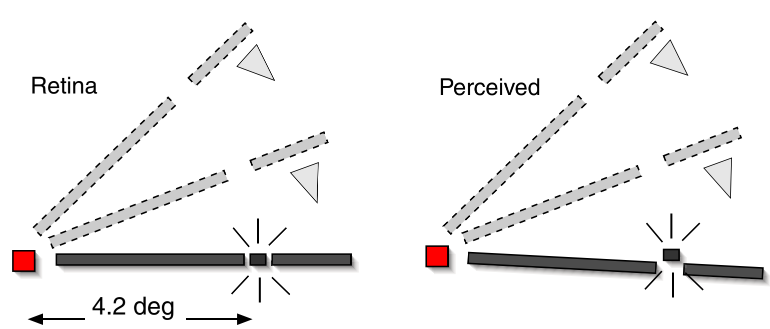

Fig. 1. Stimulus used in Experiments 1 and 2. The initial position of the moving bar was set at random before starting move. The red fixation point was placed at the center of the screen. See text for more details. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this paper.)

started the next trial. A third condition (*variable interval*) was identical to the self-triggered condition except for the fact that the time at which the flash appeared after the key press was randomly (uniform distribution) varied in the range [0.2–1.2] seconds. A fourth condition (*auditory*) was identical to the control condition except for the fact that the appearance of the flash (between 2.5 and 5.8 s after motion onset) was predicted by a sound that was played 300 ms earlier than the flash.

The four conditions were presented in different sessions (three sessions per condition), with a different order for the four subjects. Each subject was presented with a total of 2592 trials: (6 velocities * 9 offsets * 4 repetitions = 1 session) * 3 sessions * 4 conditions. The order of the conditions was randomized across subjects.

2.1.4. Data analysis

The percent of flash leading (ahead) responses was pooled over subjects and a cumulative gaussian was fitted by minimizing the mean square error. The mean of the gaussian gives us the point of subjective equality (PSE) and the deviation gives us the sensitivity. The PSE reflects the amount of FLE. The larger the PSE, the higher the FLE. To obtain the confidence intervals of these two parameters (mean and deviation) we used bootstrap (Efron & Tibshirani, 1993) as conducted by Kanai et al. (2004). This procedure was applied for two independent variables: the spatial offset and the temporal offset. When conclusions could not be drawn by merely looking at the overlap between two confidence intervals, parametric bootstrap and Monte Carlo simulations were used to compare two given psychometric curves by testing the null hypothesis that the observed difference between the two PSEs (or the two slopes) is not different than zero. To accomplish this, we used the same procedure as that implemented in pfcmp (Wichmann & Hill, 2001a, 2001b), but, we computed a bootstrap p value independently for each parameter, instead of a combined (PSE and slope) one as was carried out in pfcmp.

2.2. Results

2.2.1. Analysis as a function of spatial and temporal offsets

Fig. 2 shows the percentage of flash-ahead responses split by velocity as a function of the angular offset between the flash and the moving bar for the four different conditions. The pattern for the *control* condition is very similar to that reported by Murakami, 2001: not only the magnitude of the FLE increased with velocity (curves are shifted to the right), but also the deviation of the fitted gaussian (the curves are shallower). A similar pattern can be observed in the *variable interval* condition. In the remaining conditions, the FLE increases with velocity, but the deviation does not.

Fig. 3 shows the same data but as a function of the temporal offset. As can be clearly seen, the data points for the different velocities are much less scattered than when they are plotted as a function of the angular offset. We fitted a different gaussian for each velocity but the confidence intervals for the mean and deviation of the curves overlapped completely. Therefore, two different angular offsets between the flash and the moving bar elicited the same percentage of ahead responses when both angular offsets correspond to the same temporal offset with respect to the moving bar. This set of patterns is consistent with an inter-

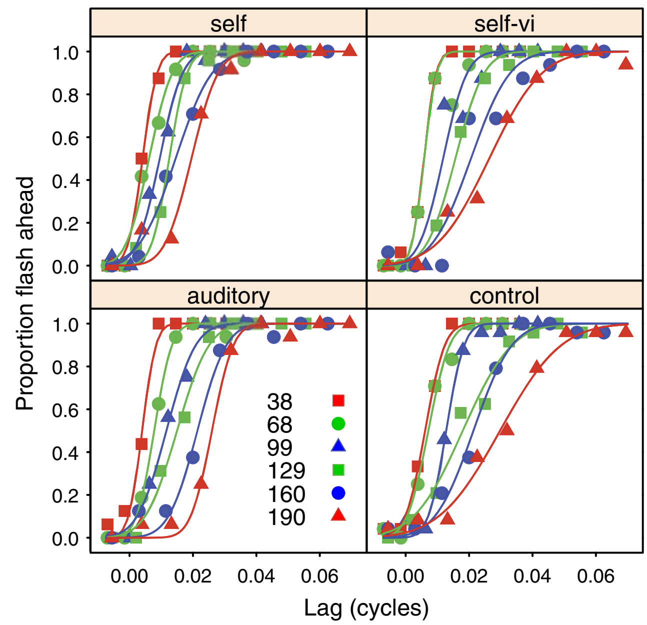

Fig. 2. Proportion of flash ahead responses as a function of the angular offset in cycles (1 cycle = 360°) between the flash and the moving bar. The different conditions are plotted in different panels. Data points are plotted separately for each velocity. The solid lines are the best fit of a cumulative gaussian.

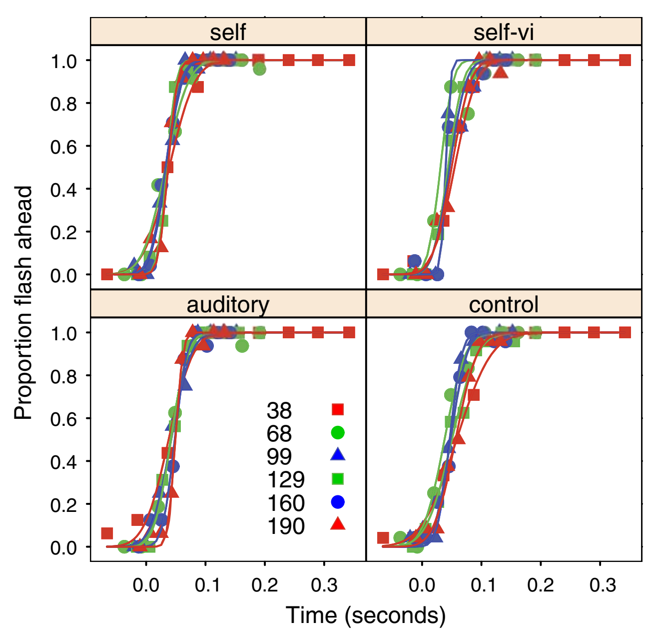

Fig. 3. The same data points as in Fig. 2, but now plotted as a function of the temporal offset between the moving bar and the flash.

pretation of the FLE as a temporal misjudgement rather than a spatial one. The magnitude of the FLE for the control condition (after averaging across velocities) is very similar (48 ms) to the one reported by Murakami (2001), who showed that the same kernel could be successfully fitted to the pattern of responses across different velocities.

2.2.2. Comparison of the different conditions

To compare the four different conditions, we pooled the data over velocities and fitted a single cumulative gaussian for each condition as a function of the temporal offset (Fig. 3). After running 2000 simulations of bootstrap, we obtained the confidence intervals for the two fitted parameters (PSE and deviation) in each condition. Fig. 4A shows the obtained PSE (mean of the fitted gaussians) for the four conditions.

With respect to the *control* condition, the magnitude of the FLE was significantly reduced only when the flash was self-triggered (48 vs. 34 ms, respectively). The obtained PSE (mean of the gaussians) for the other conditions were not significantly different from the control condition. The 95% confidence intervals clearly overlap. Although the PSE for the *auditory* (external prediction) and *variable interval* conditions were smaller than the *control* condition, these differences were not significant ($p = 0.098$ and 0.15, respectively).

Fig. 4B shows the deviation of the fitted gaussian for the four conditions. In the self-triggered condition not only the PSE, but also the variability decreased. This reduction was significant with respect to the control condition ($p < 0.001$) as it was when the flash was externally cued by the beep ($p = 0.004$). This means that while the external cue did not reduce the mean localization error (PSE is not different from the control condition), it helped observers improve their sensitivity in discriminating different temporal offsets between the flash and the moving bar (steeper curve when the beep was present). In the variable interval condition, the deviation was smaller than the control condition, although this difference was not significant ($p = 0.11$). Therefore, when the flash was not perceived as a sensory consequence of one's own action (*variable interval* condition), neither the magnitude of the FLE nor the deviation was reduced. This condition did not differ from the *control* condition.

2.3. Discussion

The results of our auditory condition show that by making the flash more (temporally) predictable, the variability of the responses was reduced. This finding is in agreement with previous work (Vroomen & de Gelder, 2004). However, the external auditory cue that we used failed to reduce the magnitude of the FLE. While some studies have found an effect of the predictability of the flash (e.g., Baldo et al., 2002; Eagleman & Sejnowski, 2000; Vreven & Verghese, 2005), others have not (e.g., Khurana, Watanabe, & Nijhawan, 2000). Vreven and Verghese (2005) also used a sound that was played at the same time of the flash and found a reduction in the magnitude of the FLE. The same result was obtained by the previously cited study of Vroomen and de Gelder (2004). These authors found a reduction of the FLE when the sound was played 100 ms before the flash. The intervals between the sound and the flash used in these studies are much shorter than the interval we used here (300 ms). Therefore, the predictive power of our external cue could have been diminished due to the duration that we used between the sound (the cue) and the flash. The lack of prediction in our auditory condition is consistent with other studies on target localization during pursuit (e.g., Rotman, Brenner, & Smeets, 2002). Rotman et al. showed that the error in localizing a flash during pursuit was not reduced by auditory or visual external temporal cues. In their study, the interval between the sound and the flash was 500 ms, even longer that the interval we used. It seems, hence, that temporal proximity is an important factor for an external cue to reduce the localization error.

The internal prediction clearly reduced the FLE. However, triggering the flash by itself does not significantly

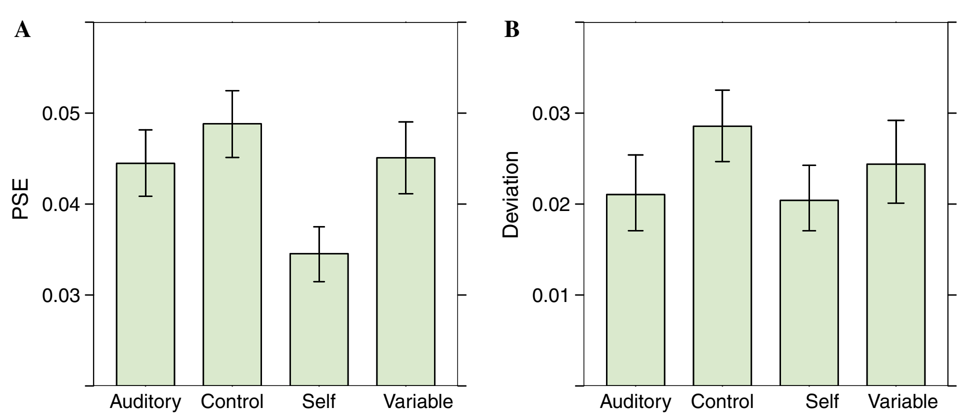

Fig. 4. (A) The obtained PSE (mean of the fitted cumulative gaussians) for each condition. To fit the curve, data points were averaged across velocities. (B) The deviation of the fitted cumulative gaussians for each condition. Error bars denote the 95% confidence interval in both panels.

reduce the FLE (*variable interval* condition). Therefore, it is necessary that the duration between the key press and the flash is held constant.

Why is the FLE reduced in the self-triggered condition? One possibility is that the key press was used as a time-marker instead of the flash itself. This possibility can be easily accommodated by Brenner and Smeets account of flash-lag (Brenner & Smeets, 2000). Their explanation of the FLE is based on the time it takes for the system to ascertain the position of the moving object once the flash has been detected. This extra-time in sampling the moving object's position would be responsible for the FLE. Therefore, it is not unlikely that the key press acted as a time-marker just before the flash was presented. If this was so, subjects, even unintentionally, could start the sampling process not at the time the flash appeared but at the (earlier) time the key had been pressed. As a consequence, they would have sampled the position of the moving object earlier in time compared with the *control* condition. Why does this possibility not account for the lack of reduction of the FLE when an auditory cue is presented? We think that, while the subject begins sampling at the time of the key press (self-triggered) because the flash is immediately available, this sampling does not occur for the beep. The relatively long duration between the beep and the appearance of the flash could therefore have discouraged the use of the beep as a time-marker. The possibility that the key press served as a time-marker is explored in the second experiment.

3. Experiment 2: Inspecting the internal prediction mechanism

In this experiment, we aim at exploring whether the reduction of the FLE observed in Experiment 1 can be attributed to a sampling strategy triggered by the key press instead of the flash itself.

3.1. Methods

Three subjects participated in this experiment, the second author and two naive subjects. All of them had normal or corrected-to-normal vision. We used the same apparatus and stimuli as in Experiment 1.

3.1.1. Procedure

The procedure was almost identical to the self-triggered flash condition of Experiment 1, except for the time-lapses between the key press and the presentation of the flash. We used three possible intervals between the key press and the presentation of the flash: 0, 16, and 32 ms. These intervals were randomly interleaved in the session. Only one of the angular velocities of Experiment 1 (129°/s) and its corresponding nine different spatial offsets were used to obtain the psychometric curve. Within each session, subjects were presented with 270 trials and each subject took three sessions.

3.1.2. Hypothesis testing and data analysis

If subjects used the key press, and not the flash as a time-marker, we would expect different FLEs for the three used time-lapses between the key press and the flash. We relied on the sample position model (Brenner & Smeets, 2000) to derive the different predictions. As long as these predictions will be derived under the assumption that subjects used the key press as a time-marker, whatever result comes out of this will only concern the role of the key press action as a time-marker for doing the task and not the position sample model as an explanation of the FLE. In other words, we are not testing the position sample model itself but using it to test whether the key press is used as a time-marker to perform the task.

Let T_p and T_f, respectively, denote the registered time-markers of the key press and the flash. If the flash, and not the key press, triggers the sampling process, then the subject will have ascertained the position of the moving object at a time $T_f + \Delta t$, Δt being the time it takes for the sampling to be completed. Let us suppose, however, that an observer starts sampling the position of the moving object at the time of the key press T_p. The subject, then, would have ascertained the position of the moving object at time $T_p + \Delta t$. If the flash is progressively delayed in time with respect to the key press then the respective relative position judgements will result in smaller FLEs because the comparisons will be made with earlier sampled positions of the moving object with respect to the time of the flash. In sum, if the key press as a time-marker is used as a strategy, we would expect different FLEs for the three time intervals. To test this hypothesis, we fitted cumulative gaussian and ran bootstrap as in the previous experiment.

3.2. Results and discussion

Fig. 5 shows the proportion of flash-ahead responses as a function of the temporal offset between the flash and the moving object split by the elapsed time between the key press and the flash. We pooled the data over all the subjects as they showed the same pattern. As can be seen, the data pattern is very clear. There is no difference whatsoever among the three different conditions. The mean FLE is 39 ms (95%-CI: 0.035–0.043) which is not significantly different from the FLE found in the self-triggered condition of Experiment 1, and is significantly different from the FLE found in the control condition of the same experiment (the 95%-CI do not overlap). Upon questioning, none of the subjects were aware of the three different time-lapses, so they always perceived the flash lag as a sensory consequence of their own action.

On the basis of the results, we cannot conclude that the key press by itself was used as a temporal marker. Another mechanism has to be responsible for the reduction of the FLE when the flash is self-triggered at a constant time, or slightly after this time.

One alternative explanation that could be proposed to explain the reduction of the FLE when the flash is internally

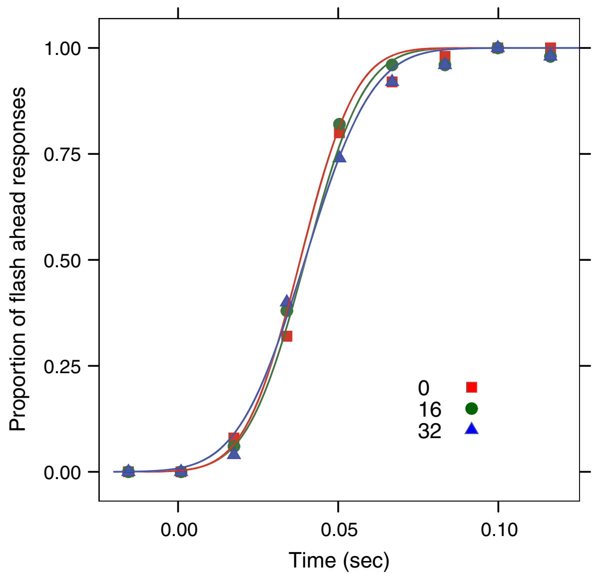

Fig. 5. Results of Experiment 2. Proportion of flash ahead responses as a function of the temporal offset between the moving bar and the flash. The data points are averaged across subjects. The solid lines denote the cumulative gaussian fits. The different symbols stand for the three different times lapses used in Experiment 2.

predicted, could be related to mechanisms that predict the sensory consequences of self-generated actions. Predicting the sensory events that are generated by our own actions is a very important capability to factor them out from the rest of the incoming sensory stream. Motor control theory suggests that the brain predicts the effect of motor commands via an efferent copy (Wolpert & Ghahramani, 2000). In addition, it has been shown that the perception of the sensory consequences of self-actions is temporally tuned (Bays, Wolpert, & Flanagan, 2005). Therefore, a comparative mechanism could have been involved in, for example, speeding up the detection of the flash when it was perceived as a sensory consequence of self-action (key press). This hypothesis would also be consistent with the finding that the perceived timing of self-generated events is moved forward in time (Haggard, Clark, & Kalogeras, 2002). If such a mechanism is responsible for the reduction of the FLE, we should be able to find the same result with longer delayed times between the key press and the flash. In other words, the narrow temporal continuities that we have used so far would not be necessary for the flash to be perceived as a consequence of the self-action. For example, Haggard et al. (2002) successfully used 250 ms between the action and the sensory consequences. In a final experiment, we test whether the causality effect is also developed when a longer delay is used.

4. Experiment 3

4.1. Methods

Three subjects, included the second author, took part in this experiment. All of them had normal or corrected-to-normal vision. We used the same apparatus as in Experiments 1 and 2. Except for small variations in the elapsed time between the key press and the flash, we used the same stimuli as in Experiment 2. The moving (129deg/s) bar appeared and a flash was self-triggered by the subjects. As before, different angular offsets were used to build the psychometric function. Within a single session, a high probable elapsed time (250 ms) between the key press and the presentation of the flash was used. There were 176 trials in each session. Eight out of these trials had a different time lapse (0 ms) between the key press and the flash presentation. The low probability trials (0 ms) were presented in random order interleaved with the high probable trials (250 ms) during the second half of the session. Subjects performed 10 sessions for a total of 1760 trials.

4.2. Results and discussion

Fig. 6 shows the proportion of flash-ahead responses as a function of the temporal offset between the flash and the moving object split by the elapsed time between the key press and the flash. Again, there are no differences between subjects, therefore data was pooled. As can be seen, while the FLE is reduced for the 250 ms condition, it was not for the 0 ms (low probability) condition. The difference between PSEs was significant (bootstrap p value of 0.01). The estimated PSE for the 250 ms is 0.36 ms with a 95%-CI of [0.356–0.038]. This PSE is not significantly different (p value of 0.767) from the FLE obtained in the self-triggered

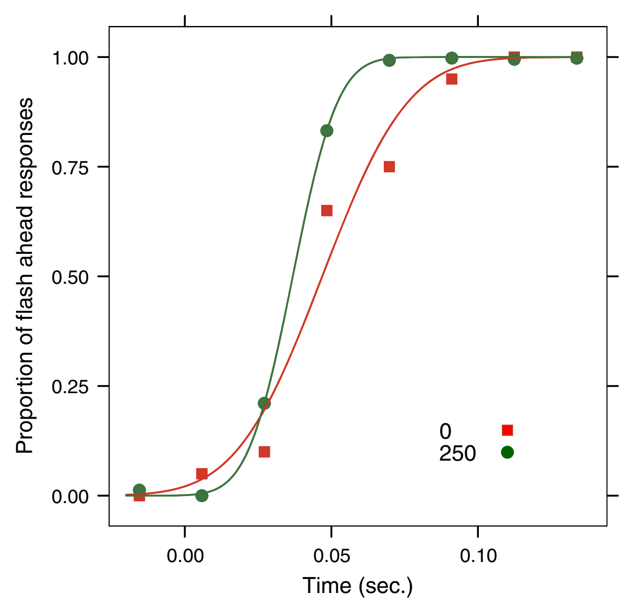

Fig. 6. Proportion of flash ahead responses as a function of the temporal offset between the moving bar and the flash. The data points are averaged across subjects. The solid lines denote the cumulative gaussian fits. Different symbols denote the different times lapses between the key press and the appearance of the flash. Solid circles denote the trials when the flash was shown 250 ms after the key press. This was the most frequent elapsed time. Solid squares denote those trials when the flash was presented unexpectedly early (0 ms).

condition of Experiment 1 (about 34 ms). The obtained PSE for the low probable elapsed time was 47 ms with a 95%-CI of [40–54], making it virtually the same as the FLE obtained in the control condition of Experiment 1 (48 ms) (p value of 0.892). We can conclude that it is not the temporal proximity between the action and the flash that matters, but the development of a causal relationship between the action and the flash as a sensory consequence due to a perceived temporal contingency.

5. General discussion

We have shown for the first time that the perception of the FLE can be modulated by our own actions. The perception of the flash as a consequence of a self-action appears to be necessary to reduce FLE. After ruling out the possibility that the key press was used as a time-marker, we think that a mechanism similar to those involved in predicting the consequences of self-actions can explain the reduction of the FLE. Of greater interest would be to explore what sort of error is reduced by this internal prediction. It is known that temporal and spatial contributions may affect the FLE Murakami, 2001. For example, the significant FLE reported under flash terminated conditions in Kanai et al. (2004) may reflect spatial mechanisms that extrapolate the moving object (Nijhawan, 1994). Apart from these spatial mechanisms acting on the moving object, temporal contributions can also be of importance. Illustrating this is the fact that the magnitude of the FLE can also be modulated by manipulating the time it takes for the flash to reach awareness, or the time it takes to sample the position of the moving object in response to the flash Brenner and Smeets, 2000. An example of the former case is the effect on the FLE found in Purushothaman, Patel, Bedell, and Ögmen (1998). These authors showed that the manipulation of the luminance of the flash has an effect on the FLE. The difference between the control condition and the self-triggered condition could be mainly attributed to a reduction of the temporal error in the process of detecting the flash. In this respect, the effect found in the present study can be closely related to the modulation of the FLE when the luminance of the flash is manipulated.

Some theories have addressed how a sensory system gets information about the stimulus (e.g., Grice, Nullmeyer, & Schnizlein, 1979; Link, 1992). Generally, these theories propose that sensory information accumulates in time until the difference between a signal and noise distribution reaches a certain threshold. An efferent copy of the key press broadcasted to sensory areas and predicting the sensory consequences could have modified (lowered) the threshold criteria. Therefore, the internal prediction could have shortened the time-course of the flash detectability. Although this explanation is similar, we claim that it cannot be considered a variant of the differential latencies explanation based on faster neural signals for moving objects when compared to static objects.

Finally, this interpretation is consistent with most accounts of the FLE. In Experiment 2, we relied on the sample position model of Brenner and Smeets, 2000 to test whether the key press was used as a time-marker giving place to a reduction of the FLE. Having ruled out this possibility, however, our findings do not necessarily undermine the explanatory power of this model, as the sample position model relies on ascertaining the position of a moving object. Our finding, we think, is better accounted for by a reduction of the detection time of the flash, leaving the contribution of the moving object to the FLE unaffected.

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